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Circulation of tapeworms of *Sorex araneus araneus* L.
in biocenosis of Białowieża National Park

Krążenie tasiemców *Sorex araneus araneus* L. w biocenozie
Białowieskiego Parku Narodowego

The parasites of *Insectivora* were and are the subject of fairly numerous studies. Among the bibliographic positions known to me this theme was elaborated by: in USA — Rausch et Kuns 1950, Oswald 1951, 1957, Locker et Rausch 1952, Neiland 1953, Voge 1953, 1955a, b, c, Voge et Rausch 1955; in Western Europe (England, Switzerland, France) — Meggitt 1924, Baer 1925, 1932, Baylis 1934, Joyeux et Baer 1936a, b, 1937, Hübscher 1937; in countries of East Europe — Skrzabin et Mathevossian 1948, Sadovskaja 1954, Spasskij 1954, Shaldibin 1957, Morozov 1957 (Soviet Union); Kobulej et Versényi 1953 (Hungary); Prokopič 1956, 1957b, c, 1959 (Czechoslovakia).

In Poland the parasites of *Insectivora* were studied by Sołtys 1952, 1954, Żarnowski 1953, 1955, Pojmańska 1957, Rybicka 1958, 1959, and Gromysz, Jarnicka et Piwowarska (in manusc.).

The main object of this work is the presentation of the routes of circulation of tapeworms in Białowieża National Park (BNP) biocenosis, and the analysis of the basic factors conditioning the variability of the degree of the intensivity of this circulation. This analysis was made on the background of the available data on the biology and ecology of the common shrew as the final host and on the hitherto known intermediate hosts (Kisielewska 1958a, b, 1959, 1960a, b).

Taking into consideration the mentioned aspects and being in possession of a comparative material collected during 6 years it seems that an attempt could be made to give not only a picture of the fauna of tapeworms of *Sorex araneus araneus* L. in BNP, but to try at least partly to throw some light on the processes to which the fauna is submitted in the given biocenosis.

Here I should like to express to Prof. Dr. W. Michajłow words of cordial gratitude for guiding my work and for the valuable informations he offered during the elaboration of the collected material. I owe also words of thanks to Prof. Dr. A. Dehnel who made accessible to me the materials collected by the Mammals Research Institute, Polish Academy of Sciences, for discussing with

me the text of this work. I am grateful to Dr. T. Pojmańska for offering me the materials collected by her during the postmortem examinations of snails conducted by her to find the larvae of trematodes.

Materials and methods

The material for the present work, cysticeroids and adult tapeworms, was collected from the common shrew (final host) and from invertebrates (intermediate hosts).

A total number of 2030 tapeworms collected from May 1953 till May 1959 were examined. Nine species of tapeworms were found; seven of them belong in the family *Hymenolepididae* Fuhrmann 1907 and two in the family *Dilepididae* Fuhrmann 1907.

7188 specimens of invertebrates were examined from June 1957 till November 1959: *Insecta* 1868 specimens, *Myriapoda* 1109 specimens, and *Gastropoda* 4211 specimens. 8 specimens of cysticeroids were found, 5 of which were identified with the adult tapeworms and 3 remained unclassified.

Experimental invasions of the common shrew with the larvae of tapeworms were made on animals kept for breeding purposes by the Mammals Research Institute. The basic diet for the bred shrews consisted of minced meat given twice a day and water. This diet was supplemented with plant food to secure in a sufficient quantity and proper proportion vitamins and other constituents (Dehnel 1949). The shrews fed in this way had no chance to become de novo invaded with tapeworms, and the parasites previously acquired in field were lost in about 6 months (Kisielewska 1960a). For security only animals kept under breeding conditions for about 1 year were used for experimental invasions.

The larvae of tapeworms were administered to the shrews in several ways.

When a small number of cysts was available and when at the same time the cysts could be easily isolated from the body cavity of the intermediate host, they were administered together with the larvae of *Tenebrio molitor* (meal worm). For this purpose the head of the larva was cut off, the cysts of tapeworms were introduced by a pipette into the body and the shrews were fed with the larvae prepared in this way. Thus exactly were administered the cysts of *Staphylocystis furcata* and *Soricinia diaphana*.

The cysts of the same species, when found in large numbers as well as the cysts of *Choanotaenia crassiscolex* were given in meat to the shrews which were on a decreased ration of meat to secure that they ate the whole portion within 12 hours.

The third way of infecting animals was the administration of cysts together with the intermediate host. In the case of tapeworms which had as their intermediate hosts insects and snails this method could not be used because it was impossible to determine the presence of the cysts avoiding complete destroying of the intermediate host. The method, however, offered very good results (100 per cent successful infections) in the case of *Pseudodiorchis prolifer*, the intermediate host of which in the BNP is the myriapod *Glomeris connexa* (Kisielewska 1960a). The larval forms of this tapeworm occur in numbers reaching at least several thousand in one host individual. To find the presence of cysts it sufficed to pierce slightly with a needle the examined myriapod. When it was infected, a stream of many tiny cysts spouted out. Such slightly injured but living myriopods were given to the shrews on a Petri dish to prevent their escape in the cage.

A total number of 27 mammals (17 *Sorex araneus araneus* L., 4 *Sorex minutus* L. and 6 white mice) was fed with the cysts of tapeworms: *Choanotaenia crassiscolex*, *Staphylocystis furcata*, *Soricinia diaphana*, *Pseudodiorchis prolifer*, and *Neoskrjabinolepis singularis*.

In the last mentioned case the result was negative, because only white mice were fed with it and the mouse is not a natural final host of this species of the tapeworm.

The results of the successful experiments are shown in Table I.

The collections of snails, myriapods and insects were submitted to postmortem

T a b l e I
Results of positive experimental invasions of mammals with cysticercoids of tapeworms

Final host	Intermediate host	Larvae exposed	Invasion method	No. cysts given	Day of		Results of autopsy
					exposure	autopsy	
<i>Sorex araneus araneus</i>	<i>Goniodiscus ruderatus</i>	<i>Choanotaenia crassicolex</i>	with meat	43	25.VI	10.VII	12 specimens with gravid proglottids
"	<i>Succinea putris</i>	"	"	18	26.VI	12.VII	9 specimens as above
"	<i>Geotrupes stercorosus</i>	<i>Soricinia diephana</i>	"	22	26.VI	12.VII	19 two- and three-serial specimens
"	"	<i>Staphylocystis furcata</i>	in meal worm	6	14.VII	5.VIII	5 specimens with gravid proglottids; eggs
"	"	"	"	9	15.VII	5.VIII	5 specimens as above
"	"	"	meat	15	16.VII	5.VIII	12 specimens as above
"	<i>Glomeris connexa</i>	<i>Pseudodiorchis proflifer</i>	in myriapod	many	20.V	7.VI	many specimens, gravid proglottids; eggs
"	"	"	"	"	26.VI	17.VII	"
"	"	"	"	"	26.VI	17.VII	"
"	"	"	"	"	28.VI	12.VII	"
"	"	"	"	"	24.VI	30.VI (died)	about 630 immature specimens
<i>Sorex minutus</i>	<i>Zonitoides nitidus</i>	<i>Choanotaenia crassicolex</i>	with meat	17	12.VII	30.VII	6 specimens with gravid proglottids
"	<i>Geotrupes stercorosus</i>	<i>Staphylocystis furcata</i>	in meal worm	8	8.VIII	27.VIII	8 specimens as above

examination to find natural infections with cysts of tapeworms. The dissections of snails were conducted by T. Pojmańska and those of myriapods and insects by myself.

A part of the invertebrates was kept under breeding conditions for the experimental infections with eggs of tapeworms. Breeding of coprophageous insects was arranged in glass dishes containing horse faeces. Humidity was maintained by the use of cotton wool soaked with water. The necrophageous species received additionally meat. Under such simple conditions the insects could be kept over two months. The myriapods were also kept in glass dishes filled with decayed leaves and rotten wood. The snails were not kept under breeding conditions.

The experimental infections with eggs of tapeworms were conducted exclusively on insects. Enigk et Sticinsky 1957 infecting insects with eggs of poultry tapeworms found that *Geotrupes sylvaticus* (syn. *G. stercorosus*) became infected rather with difficulties, especially those individuals which were kept for some time under breeding conditions. In the present work I encountered no difficulties of this kind. The specimens to be infected were kept overnight in empty, sufficiently humid jars. The starved insects devoured the proglottids given on the bait (small portions of minced beef) within several minutes.

Enigk et Sticinsky 1957 attained in their work on experimental infection an intensivity of invasion reaching 300 larvae. They suggest that to make infection successful the insects should be brought in touch with the eggs of tapeworms repeatedly, several times day after day. The intensivity of invasion in my experiments was 3—12 larvae. The insects were given fairly large portions of gravid proglottides filled up with eggs, but were never infected repeatedly.

The infected insects were dissected every second day starting from the moment of infection, each time 2—3 specimens were examined. The dissections were initiated at such an early period and were so often repeated with a dual purpose: (a) In case of a positive result of invasion it enabled to trace and consequently to reconstruct the successive stages of the formation of the given larval form in the body of the host; (b) Successive dissections supplying the gradually growing and more and more advanced larvae in their development offered a verification that the larvae take really origin from the experimental infection. Besides, only insects which remained under breeding conditions not shorter than at least two weeks were used in the experiments. This period of time was long enough for all the larvae from an eventual natural infection to attain the form of the cysticeroid.

Table II
Results of experimental invasion of insects with tapeworm eggs

Tapeworm species	Species of invaded insects							
	<i>Geotrupes stercorosus</i>		<i>Necrophorus vespilloides</i>		<i>Silpha sinuata</i>		<i>Pterostichus vulgaris</i>	
	No. of		No. of		No. of		No. of	
	cont.	invad.	cont.	invad.	cont.	invad.	cont.	invad.
<i>Staphylocystis furcata</i>	20	14	10	0			10	0
<i>Soricinis diephani</i>	40	31	5	0	5	0		
<i>Neoskrjabinolepis singularis</i>	15	0			5	0		
<i>Choanotaenia crassicolex</i>	10	0			5	0		
Total	85	45	15	0	15	0	10	0

Positive results were achieved only when the proglottids with eggs were given to the insects 1—5 hours after they were removed from the final host (after Enigk et Sticinsky 1957). The data are illustrated in Table II.

The adult forms of the tapeworms were classified on the basis of permanent preparations, the measurements were taken both on preparations and on fresh material in cases when the species of the tapeworm rose no doubt. The cysticeroids and earlier developmental forms of tapeworms were measured, photographs were taken and the figures were drawn only from live specimens.

TAPEWORMS OF THE COMMON SHREW

Sołtys 1952 found in the common shrew of the BNP the following species of tapeworms: *Hymenolepis singularis*, *Dicranotaenia furcata*, *Ditestolepis diaphana*, *Vigisolepis spinulosa*, *Choanotaenia crassiscolex* and *Ch. hepatica*.

The materials examined by me proved that the list requires some supplements, because 9 species of tapeworms were found. Four of them will be described separately as found for the first time in the BNP. The species *Choanotaenia hepatica* (Baer 1932) described by Sołtys in his material was, however, not discovered.

Hymenolepididae Fuhrmann 1907

A critical discussion of the systematic conceptions of the family *Hymenolepididae* was not planned in the present work. As before, I am using Spassky's system to preserve nomenclative uniformity with my works on life cycles of tapeworms belonging to this family (Kisielewska 1958 b, 1959, 1960a, b).

(1) *Staphylocystis furcata* (Stieda 1862) Spassky 1950

This species occurs in the BNP in the common shrew (Sołtys 1952, Kisielewska 1959) and in one case it was found in *Neomys fodiens* (Sołtys 1954). The morphology of the specimens found by me is in agreement with the description presented by Żarnowski 1955 and Rybicka 1959.

Measurements of the tapeworms according to my findings: length 16—18 mm., width 0.942—1.007 mm. Diameter of scolex 0.25—0.30 mm., suckers 0.061—0.101 mm., width of rostellum 0.086—0.092 mm. Number of hooks 24—28, length of hooks 0.022—0.028 mm. Diameter of testes in younger proglottids 0.04—0.05 mm., in older 0.071—0.094 mm. Length of cirrus pouch 0.138—0.152 mm.

According to Żarnowski 1955, his material shows a distinct subdivision into two groups of individuals. The first of them is typical to *Sorex araneus araneus* (15—20 hooks, 0.017—0.019 mm. in length), the second — to *Crociodura leucodon* (24 hooks, 0.023—0.026 mm. in length). Sołtys 1952 and Kisielewska 1959 proved that in the BNP this species from *Sorex araneus araneus* has such measurements and such a number or even a greater number of hooks as in the environs of Puławy have the individuals typical to *Crociodura leucodon* (this mammal does not occur in the BNP). Similarly Rybicka 1959 makes the statement that the individuals found by her in the Kampinos Wilderness in *Sorex araneus araneus* are typical of the group described by Żarnowski to *Crociodura leucodon*.

In the developmental cycle of *S. furcata* there appears the cysticercoïd found for the first time by Linstow in 1893 in *Geotrupes sylvaticus*. In the BNP I found the cysticercoïds in *G. stercorosus* (syn. *G. sylvaticus*) and in *Pterostichus vulgaris*. This cycle was by me verified by way of experimental infections (Kisielewska 1959).

(2) *Neoskrjabinolepis singularis* (Cholodkovsky 1912)
Spassky 1954

In the BNP this species occurs in *Sorex araneus araneus* (Soltyś 1952, Kisielewska 1958b), *S. minutus* and in *S. macropygmaeus karpiński* (Soltyś 1954).

The morphology of the tapeworms in my material is in accordance with the description given by Soltyś 1952, Żarnowski 1955, Pojmańska 1957 and Rybicka 1959. The analysis of the testes studied by me confirms once again the arrangement of the testes in one row and the more or less marked serial appearance of the strobila (Soltyś 1952, Żarnowski 1955).

Measurements of the tapeworms in my material: length 3.8—4.9 mm., width 0.294—0.317 mm. Width of scolex 0.176—0.275 mm., suckers 0.079—0.089 mm., number of hooks 10, length of hooks 0.035—0.043 mm. Diameter of testes in mature segments 0.040—0.049 mm.

The developmental cycle is not yet precisely known. The cysticercoïds were found in one case in an insect of the genus *Catops* (Kisielewska 1958b). The characteristic shape of the hooks, their constant number and the form of the scolex made it possible to identify these larvae with the mature form of *N. singularis*.

(3) *Soricina diaphana* (Cholodkovsky 1906) Żarnowski 1955

In the BNP this species occurs in *S. araneus araneus* (Soltyś 1952, Kisielewska 1960b), *S. minutus* and *S. macropygmaeus karpiński* (Soltyś 1954).

The strobila (2.898—3.831 mm. in length) is characterized by a distinctly marked subdivision into three series, each of which possesses proglottids uniformly advanced in development. The first series contains 24—30 immature proglottids. Its maximal width 0.077—0.111 mm. The second series contains 21—29 segments with a mature reproduction apparatus. Maximal width of this series 0.125—0.214 mm. The third series (18—30 segments, maximal width depends on the degree of development and fluctuates from 0.175—0.628 mm.) contains uterine segments. In the earlier developmental stage of this series the borders between the separate segments are clearly preserved. Subsequently the segments as well as the uterus unite together and form a syncapsule, which tears off easily from the strobila. In case the syncapsule is ruptured, the eggs pour out and form a compact packet (Fig. 1b).

The remaining dimensions: scolex 0.118—0.141 mm. in length, width 0.172—0.196 mm.; suckers of diameter 0.125—0.128 mm. On the scolex the trace of rostellum is marked, considerable better visible on fresh material than on fixed preparations. Larval forms (scolices of cysticercoïds and earlier forms before invagination) are provided with an involuted but quite marked rostellum which in some species shows even slight movements (Kisielewska 1960b). On this basis it can be supposed that the regression of the rostellum in this species is a secondary phenomenon.

Among the authors describing this species there is a difference of opinion as to the number of testes. Cholodkovsky 1906, Kobulej et Ver-sényi 1953, Kobulej 1953, Żarnowski 1955, Prokopič 1957, Gro-

mysz (in litt.) found three testes. According to Sołtys 1952 this species is provided with two testes and therefore he created for it the genus *Ditestolepis* Sołtys 1952. Sołtys' data are corroborated by Rybicka 1959 who supports the necessity to preserve the genus *Ditestolepis*. I saw in my material three

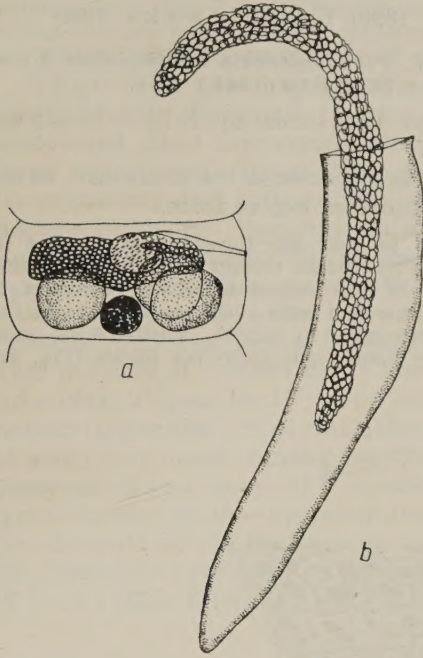


Fig. 1. *Soricinia diaphana*: a — Mature proglottis from the second series of strobila; b — Third series of strobila, burst syncapsule with eggs packet

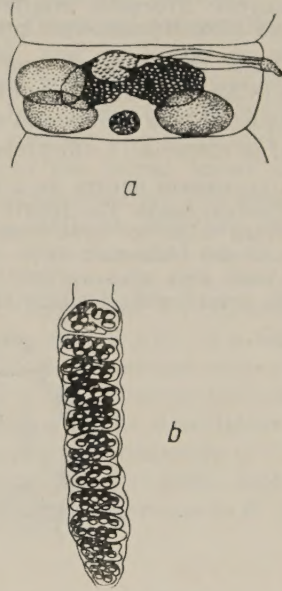


Fig. 2. *Soricinia tripartita*: a — Mature proglottis from the second series of strobila; b — Third series of strobila, gravid proglottides joined

(4) *Soricinia tripartita* Żarnowski 1955

testes (one poral, two aporal), whereby the location of the aporal testes, one above the other makes it often difficult to trace them (Fig. 1a). The oblong diameter of the testes is 0.026 — 0.034 mm., the length of the cirrus pouch 0.084 — 0.098 mm.

The intermediate host in the BNP is *Geotrupes stercorosus*, confirmed under natural conditions and verified experimentally (Kisielewska 1960b).

This species was in the BNP found for the first time in *S. araneus araneus* L.

The strobila is characterized by a marked three series arrangement. I found beside individuals with immature uterine segments of the third series also such ones in which the mature segments of this series confluent together (Fig. 2). Żarnowski 1955 and Rybicka 1959 found only individuals with immature uterine segments, i. e., not joined together.

The scolex measures 0.087 — 0.091 mm. in length and 0.145 — 0.185 mm. in width. Suckers 0.150 — 0.190 mm. $\times$ 0.095 — 0.106 mm.

The structure of the second series of segments corresponds to the description given by Żarnowski 1955. In my material the diameter of the testes was 0.032—0.049 mm. and the length of the cirrus pouch 0.068—0.094 mm.

The development cycle is not known.

(5) *Pseudodiorchis prolifer* (Villot 1890) Kisielewska 1960

Synonyms: *Urocystis prolifer* Villot 1890, *Pseudodiorchis multispinosa* Żarnowski 1955, *Hymenolepis prolifer* (Villot 1890) Stammer 1956.

In BNP this species was found for the first time by Kisielewska (1960a) in *Sorex araneus araneus* L.

Because this is the second description of this species in the literature, based on a large material, I am presenting it in a more extensive form.

This tapeworm occurs as a rule in several to over ten thousand specimens in the individual hosts. The length of the strobila fluctuates within 0.524 to 1.071 mm., width from 0.122 to 0.164 mm. The number of the segments of the strobila is 19—49. Scolex (diameter 0.124—0.182 mm.) is provided with suckers of the diameter 0.054—0.063 mm. and a rostellum 0.020—0.028 mm. in length, 0.040—0.064 mm. in width, armed with a single crown of closely contiguous fork-like hooks (Fig. 3a)

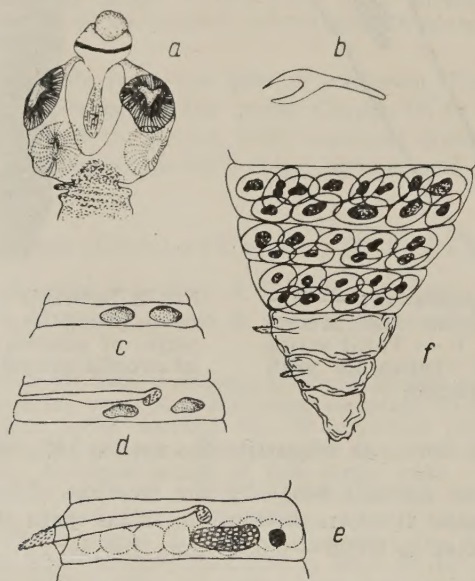


Fig. 3. *Pseudodiorchis prolifer*: a — Scolex; b — Imaginal hook; c—e — Development of genital organs; f — Terminal gravid proglottides

which at a lower magnification appear as a uniform ring, 0.020 mm. in diameter. The number of hooks about 120, their length 0.005—0.006 mm. Żarnowski 1955 reports that the rostellum is surrounded by a single row of rod-like hooks. In my material a similar picture was observed, but the observations on the live mature individuals and cysticercoids proved that the shape of the hooks is forky. When the rostellum is drawn in into the cirrus pouch, on the top of the scolex a funnel is formed which gives an appearance of the presence of a fifth, terminal sucker.

In the first segments, directly following the scolex (Fig. 3b), two testes can be observed. Their diameter is 0.008—0.012 mm., and they are located in one row, slightly displaced towards the aporal part of the segments. In the further segments there appears cirrus pouch, 0.037—0.046 mm. in length; cirrus covered with spines. In segments with developed female sexual organs there is a centrally located ovary and a spherical vitelline gland, smaller than the ovary, and located aporally in relation to it (Fig. 3 c—e). The uterus, which in the terminal segments occupies the whole interior part of them, contains 8—16 eggs. The three or four last segments are distinguished by an atrophy of parenchymal and muscular elements.

Stammer 1956 reports that he found in *Glomeris hexasticha* larvae identical with *Urocystis prolifer* Villot 1890, and in *Sorex araneus* he discovered adult tapeworms which he connected with the mentioned larval form and named *Hymenolepis prolifer* (Villot 1890) Stammer 1956. Unfortunately the author gives no description neither any drawings of the mature tapeworm, therefore only on the basis of the larval forms one can suppose that he dealt with the species *Pseudodiorchis prolifer*. The lack of the mentioned description makes also the discussion difficult, whether the tapeworm found by Stammer was correctly by him classified to the genus *Hymenolepis*. The genus *Pseudodiorchis* Skrjabin et Mathevossian 1948 includes at present the following species of tapeworms: *P. reynoldsi* (Jones 1944), *P. prolifer* (Villot 1890), and *P. kampinosi* Rybicka 1959. The named tapeworms are of small dimensions, their scolex is armed with a crown of many tiny hooks. Among the internal organs a differentiating feature is the presence of two testes. If it is accepted on the basis of the description of the larval forms that the tapeworm found by Stammer corresponds to *P. prolifer*, it should not, as the twotesticular parasite, remain in the genus *Hymenolepis*. Therefore I am treating the name *H. prolifer* as synonymous to *P. prolifer* (Villot 1890) Kisielewska 1960.

(6) *Vigisolepis spinulosa* (Cholodkovsky 1906)

In the BNP this species occurs in *Sorex araneus araneus*, *S. minutus*, and *S. macropygmaeus karpinskii*.

The morphology of the tapeworm is in accordance with the description reported by Rybicka (1959).

Dimensions of the tapeworm (the authoress' data): length 11—27 mm., width 0.24—0.41 mm. Diameter of scolex 0.196—0.288 mm., suckers 0.082—0.101 mm., rostellum 0.112—0.135 mm. in length and 0.062—0.074 mm. in width. Large hooks, 16—18 in number, measure 0.031—0.033 mm., small hooks (on the collum of the rostellum) measure 0.011 mm. The testes in young segments 0.050—0.057 mm., in old ones 0.081—0.087 mm. The length of the cirrus pouch 0.202—0.214 mm.

The developmental cycle unknown.

(7) *Hymenolepis* (s. l.) *scutigera* (Dujardin 1845)

I found this species in the BNP for the first time in *Sorex araneus araneus* L.

The general shape and structure correspond to the descriptions of Żarnowski 1955 and Pojmańska 1957. Small differences concern the following details of the structure: the cirrus pouch extends to the one half of the segment (according to Żarnowski it is shorter, according to Pojmańska

it extends over the one half of the segment), the sexual pores are located in the front half of the lateral margin of the segment, in accordance with the data of Żarnowski (according to Pojmańska — in the one half of the segment), the relation of the width to the length of the mature uterine segments is as 1:4 to 1:6 (according to Żarnowski 1:4, according to Pojmańska 1:3).

Measurements of the tapeworm (the authoress' data): strobila 6.8—9.9 mm. in length and 0.186—0.218 mm. in width. Scolex 0.127—0.263 mm. in width, diameter of suckers 0.115—0.132 mm., number of hooks 10, length of hooks 0.032—0.034 mm. Diameter of testes in young segments 0.016—0.018 and in old ones 0.033—0.037 mm. Length of cirrus pouch 0.049—0.054 mm.

The developmental cycle unknown.

Dilepididae Fuhrmann 1907

(8) *Choanotaenia crassiscolex* (Linstow 1890)

This species occurs in the BNP in *S. araneus araneus*, *S. minutus*, *S. macro-pygmaeus karpinskii*, and *Neomys fodiens*.

The morphology is in accordance with the descriptions of Żarnowski 1955, Pojmańska 1957 and Sołtys 1952.

Measurements of the tapeworm (the authoress' data): strobila 14—15 mm. in length and 0.58—1.25 mm. in width. Scolex 0.54—0.72 mm. in width, suckers $0.42-0.64 \times 0.10-0.15$ mm., length of rostellum 0.42—0.59 mm. Number of hooks 18, length of hooks 0.048—0.056 mm. Number of testes 11—18, diameter of testes 0.047—0.067 mm., length of cirrus pouch 0.185—0.198 mm.

The tapeworm passes in its life cycle through various species of terrestrial snails (Kisielewska 1958a).

(9) *Dilepididae* sp.

I found in *Sorex araneus araneus* young tapeworms (Fig. 4a) which I classified to the family *Dilepididae* on the basis of the morphology of the scolex. These forms have scolices provided with developed holdfast organs, very broad and short, not segmented body or rudiment of strobilization. The lack of segments with reproductive organs made an accurate classification of these forms impossible.

The length of the body is 2.0—2.5 mm., width of scolex 0.475—0.527 mm. Suckers measure 0.105—0.114 $\times$ 0.160—0.162 mm. Rostellum short and broad (0.209 mm.), armed with a double crown of 52—56 hooks; the large hooks measure 0.087 mm., the small ones 0.075 mm. (Fig. 4b, c).

Taking into consideration always the same degree of the development of these forms (the head stage, or the beginning of strobilization) and their habitus (intestinal lumen), it can be supposed that micromammals play to this species of tapeworm the role of transmitters, or reservoir hosts, but no definite stage of development takes place in them. They would, therefore, play solely the role of the lacking link in the alimentary chain between the micromammals, in which most likely the cysticercoids develop, and some natural enemy of the micromammals in which develops the mature form of the described tapeworm producing eggs.

Similar forms were found by Soltyš 1954 in the BNP in *Sorex araneus araneus*, Rybicka 1959 in the Kampinos Wilderness in *S. araneus araneus*, and Prokopič in Czechoslovakia in *Neomys fodiens*. Prokopič classified them to the species *Dilepis undula* (Schrank 1788), the



Fig. 4. *Dilepididae* sp.: a — Total shape; b — Imaginal hook of the 1st row; c — Imaginal hook of the 2nd row

cysticercoids of which develop in the insects of the genus *Geotrupes*, and expressed the supposition that these forms were an example of the passage of tapeworms from one intermediate host, invertebrates, to other intermediate host, vertebrates, what is a phylogenetically higher degree of adaptation.

CIRCULATION OF TAPEWORMS

The developmental cycle of *Hymenolepididae* and *Dilepididae* runs most commonly with the participation of one intermediate host in which the larval form of the cysticercoid type is developed. It is only in few cases that a simple development is present without an intermediate host. As an example can serve *Hymenolepis erinacei* (Gmelin 1789) (Joyeux 1921, 1927).

Among the tapeworms parasitizing *S. araneus araneus* all the species with known developmental cycle possess one intermediate host.

In the ontogenic development the parasites live successively in three various environments. The first of them is the external environment. This environment is only a terrain on which the intermediate host takes the invasive oncosphere in. The oncosphere imprisoned in the egg membranes is not adapted to take active part in it, it cannot attack the host. However, there may occur certain circumstances which increase the chances of the eggs to reach the organism of the intermediate host. In the case of the discussed tapeworms it can be supposed that such a chance is increased to a considerable degree by the fact that the eggs are removed together with the faeces of mammals and that the faeces constitute the natural food to many species of invertebrates, especially coprophagous ones.

In the next two environments, formed by the body cavity of the intermediate host and the intestine of the final host, there occurs a certain part of ontogenesis which leads to the development of cysticercoids and adult tapeworms.

1. Intermediate hosts, their biology and invasion with larvae of tapeworms

In searching after natural intermediate hosts of the tapeworms of the common shrew in the BNP I accepted as the starting point the data in the literature referring to: (a) the food of the common shrew, (b) already solved life cycles of other species of tapeworms which possessed their intermediate hosts among terrestrial invertebrates.

Dehnel 1949 and Borowski et Dehnel 1952 report that the basic food of the common shrew in spring, summer and early autumn are insects, larvae of insects, earthworms etc. Tupikova 1949 states that, under breeding conditions, they eat almost everything, although *Homoptera*, *Carabidae* and tritons constitute a small part in their food. Pelikan 1955 found in the stomach of *Soricidae* chitin parts of insects and snails, larvae of insects, earthworms, micromammals and seeds. Seeds were found exclusively in winter, when the majority of the invertebrates is hidden deeply in the ground. According to this author, however, seeds constitute only a supplement to the poor animal diet in winter.

The data from the parasitological literature indicate that *Coleoptera*, *Hymenoptera*, *Lepidoptera* and other insects, *Gastropoda*, *Myriapoda* and *Oligochaeta* are intermediate hosts of tapeworms of mammals and birds.

Tree groups of invertebrates (myriapods, snails and insects) were taken into consideration in the BNP.

(a) *Myriapoda*

Glomeris connexa,* the most common myriapod in the BNP, proved to be the intermediate host of *Pseudodiorchis prolifer* — Kisielewska 1960a.

Out of 1047 *G. connexa*, 104 (9.9%) specimens were invaded. Table III illustrates the extensiveness of invasion in the separate months of the year. The intensivity of invasion was several thousand larvae in one myriapod.

There were also made 62 dissections of myriapods of the genus *Julus* but with a negative result.

* I owe words of thanks to Prof. Dr. H. Jawłowski for the classification of *Myriapoda* collected by me.

Table III
Degree of invasion of *Glomeris connexa*
with larvae of *P. prolifer*

Month	Year	Exam.	Invad.	%
V	1958	148	11	8.1
VI	1957	6	0	
	1958	208	12	5.8
	1959	291	21	7.2
VII	1957	33	4	12.1
VIII	1957	17	1	5.9
	1958	38	4	10.5
	1959	218	36	16.5
IX	1958	58	11	18.9
XI	1957	30	4	10.3

Table IV
Degree of invasion of snails with cysticercoide of *Ch. crassiscolex*

Species and family of snail	1957				1958			
	Exam.	Invad.	%	Month *	Exam.	Invad.	%	Month *
<i>Succinea putris</i> (L.), Succineidae	329	3	0.9	VII, XI	1170	25	2.0	V to X
<i>Cochlicopa lubrica</i> (Mull.), Cochlicopidae	19	1	5.3	XI	13	2	15.3	VI, VIII
<i>Vitrina pellucida</i> (Mull.), Vitrinidae	13	9	69.2	XI				
<i>Eulota fruticum</i> (Mull.), Eulotidae	154	1	0.6	IX	166	2	1.2	VIII, IX
<i>Zonitoides nitidus</i> (Mull.), Zonitidae	531	9	1.7	VI, VII	193	5	2.5	VI, VIII
<i>Vitrea contracta</i> (West), Zonitidae	2	1		VII				
<i>Goniodiscus rotundatus</i> (Mull.), Endodontidae	165	0	0		53	1	0.5	VI
<i>Goniodiscus ruderatus</i> (Stud.), Endodontidae	159	5	3.1	VI, VII, XI	119	2	1.6	V, VI
<i>Clausilla ventricosa</i> (Drap.), Clausiliidae					18	1	5.6	VI
<i>Lacineria plicata</i> (Drap.), Clausiliidae					30	2	6.6	V, VI
Clausiliidae sp.	296	3	1.0	VI, VII				

* Months, in which cysts were found

(b) *Gastropoda*

Pulmonata play in BNP a very essential part as the intermediate link in the developmental cycle of *Choanotaenia crassiscolex*. The cycle was described in a separate paper (Kisielewska 1958a).

The data concerning the degree of invasion of the separate snail species with cysts of *Choanotaenia crassiscolex* are shown in Table IV.

Beside the species listed in Table IV the following snail species were also examined but the cysts of *Ch. crassiscolex* were not found: *Pertoratelld bidens* (Chemn.) — *Helicidae* (491 dissections in 1957 and 198 dissections in 1958), *Zenobiella rubiginosa* (Schm.) — *Helicidae* (11 and 11, resp.), *Carychium minimum* Müll. — *Ellobidae* (0 and 8), *Euconulus fulvus* (Müll.) — *Ariophantidae* (20 and 9), *Vitrea cristallina* (Müll.) — *Zonitiidae* (13 and 12), *Cochlodina laminata* Mont. — *Clausiliidae* (0 and 62), and *Iphigena latestriata* (Bielz) — *Clausiliidae* (0 and 46 dissections).

(c) *Insecta*

Among the insects occurring in the BNP, the representatives of the group *Coleoptera*, particularly the family *Scarabeidae* were taken first of all into consideration. They are coprophagous (*Geotrupes*, *Aphodius*) or necrophagous (*Necrophorus*). This way of preying seemed to create particular possibilities of frequent contacts with eggs and mature segments of tapeworms.

A total number of 1868 dissections of the following insects were made*:

	spec.
(a) <i>Scarabeidae</i> : <i>Geotrupes stercorosus</i> (Scriba)	963
<i>Geotrupes stercorarius</i> (L.)	130
<i>Necrophorus vespilloides</i> (Herbst)	161
<i>Necrophorus vespillo</i> (L.)	12
<i>Necrophorus humator</i> Oliv.	30
<i>Aphodius</i> (<i>Colobopterius</i>) <i>subterraneus</i> L.	116
<i>Aphodius</i> (<i>Acrossus</i>) <i>rufipes</i> L.	1
<i>Aphodius</i> (<i>Volinus</i>) <i>melanosticus</i> Schmidt	110
<i>Aphodius</i> (<i>Aphodius</i>) <i>fimetarius</i> (L.)	82
<i>Aphodius</i> (<i>Bodilus</i>) <i>rufus</i> (Müll.)	2
<i>Licola lugubris</i> Herbst.	1
(b) <i>Carabidae</i> : <i>Carabus glabratus</i> Payk.	44
<i>Carabus nemoralis</i> Müll.	14
<i>Carabus</i> (<i>Procrustes</i>) <i>coriaceus</i> L.	2
<i>Carabus hortensis</i> L.	60
<i>Cychrus caraboides rostratus</i> Fabr.	6
<i>Pterostichus strenuus</i> (Panz)	9
<i>Pterostichus vulgaris</i> L.	26
<i>Harpalus tardus</i> (Panz)	23
<i>Amara</i> (<i>Zezea</i>) <i>plebeja</i> (Gyll.)	1
<i>Agonum gracile</i> (Gyll.)	16
(c) <i>Catopidae</i> : <i>Catops</i> sp.	2
(d) <i>Sylphidae</i> : <i>Silpha</i> (<i>Thanatophilus</i>) <i>sinuata</i> Fabr.	33
(e) <i>Hydrophilidae</i> : <i>Spheredium bipustulatum</i> F.	3
(f) <i>Staphylynidae</i> sp. sp.	6

* I should like to thank Mr. A. Golian from the Zoological Institute, Polish Academy of Sciences, for the classification of my material and for the indications concerning its collection.

The larvae of tapeworms were found in three insect species: *Geotrupes stercorosus* (larvae of *Staphylocystis furcata* and *Soricinia diaphana*), *Pterostichus vulgaris* (larvae of *Staphylocystis furcata*), *Catops* sp. (larvae of *Neoskrjabinolepis singularis*).

In *Geotrupes stercorosus*, *Necrophorus vespilloides* and *Silpha sinuata* three kinds of cysts hitherto not classified (Fig. 5) were also found.



Fig. 5 a, b. *Cysticeroid* sp. from *Necrophorus vespilloides*: a — Total shape; b — Imaginal hook; c, d — *Cysticeroid* sp. from *Silpha sinuata*: c — Total shape, d — Imaginal hook; e — *Cysticeroid* sp. from *Geotrupes stercorosus*

Geotrupes stercorosus (Scriba)

The dissections were conducted from June till November, 1957, from May till September, 1958, and in May, June and August 1959.

G. stercorosus seemed to be especially suitable to be an intermediate host of the tapeworms of *Insectivora*, because it is: (a) a species numerously represented in the BNP (Borowski 1960), (b) a fairly common food of the common shrew (Borowski et Dehnel 1952, Borowski 1960), (c) as a coprophagous species it has chances to become infected with eggs of tapeworms removed with the faeces of the shrew.

The larvae of tapeworms were found in 172 specimens, what makes 17.8%. There were found individuals invaded simultaneously with two or three species of larvae, whereby the larvae by their appearance and the degree of development did not show a negative effect of this coexistence. The cysts of tapeworms were found exclusively in the abdomen lying loosely among the internal organs. Several times the cysts of *Soricinia diaphana* were found attached to the external wall of the intestine.

The high extensiveness of invasion with the larvae of *Staphylocystis furcata* and *Soricinia diaphana* (10%) and the high intensivity of invasion prove that this insect is the proper intermediate host of these parasites, and is so far the only one known.

The relatively large material enabled to make an analysis of the extensiveness of invasion of *G. stercorosus* in the various months of the year (Table V).

Table V
Extensiveness of invasion of *G. stercorosus* in various months with cysts
of individual tapeworm species

Month	Year	No. of		%	Staphylocystis furcata		Soricinia diaphana		Undetermined cysts	
		exam.	invad.		No.	%	No.	%	No.	%
V	1958	6	1	16.7	1	16.7				
	1959	9	1	11.1	1	11.1				
VI	1957	6	0							
	1958	145	14	9.6	8	5.5	5	3.4	2	1.3
	1959	182	16	8.7	11	6.0	9	4.8		
VII	1957	105	18	17.1	5	4.7	13	12.3		
	1958	25	6	24.0	4	16.0	3	12.0		
VIII	1957	133	28	21.0	18	13.5	14	10.5	4	3.0
	1958	139	38	27.3	24	17.2	20	14.3	4	2.9
	1959	98	31	31.6	26	26.5	22	22.4		
IX	1957	22	1	4.5	1	4.5	1	4.5	1	4.5
	1958	41	14	34.1	8	19.5	10	24.5	2	4.5
X	1957	51	4	7.8	2	3.9	2	3.9		
Total		962	172	17.9	109	11.3	99	10.2	13	1.3

The table shows that June, September and October are characterized by lower extensiveness of invasion, but July and August — by a high one. The exception was September 1958, when the insects were collected during the first decade of the month, therefore theoretically this material could be included to the data of August.

It is characteristic that in periods, when the summer and autumnal intensity of occurrence of *G. stercorosus* is observed (June, September), the percentage of invasion of beetles with larvae of tapeworms drops. It seems that this phenomenon can be explained by the fact that young, not infected imagines which leave the conglomerates, „rarefy” the already invaded population of beetles and thus contribute to the decrease of the general percentage of the extensivity of invasion.

Pterostichus vulgaris L.

Out of 26 examined specimens in one of them 7 larvae of *Staphylocystis furcata* were found. *Carabidae* are predatory insects, preying on smaller insects or their larvae, have large dimensions, very hard chitin coat, ability of fast movement, and produce a caustic fluid of a paralysing effect. This way of preying and the kind of food do not favour permanent contacts with eggs of tapeworms, and these insects are not the favour food for the common shrew (what was observed also by Tupikova 1949). Although *P. vulgaris* is a small insect, and its chitin coat is less massive than in other *Carabidae*, it seems to me that it plays rather a role of a secondary or accidental intermediate host of tapeworms.

Catops sp.

In one of the two examined representatives of the genus *Catops* numerous larvae of *Neoskrjabinolepis singularis* were found. It is impossible to make an analysis as to the role of this insect in the transmission of the larvae of tapeworms. It seems, however, that the way of life of *Catopidae* (they are living and undergoing their whole development in nests of birds and mammals) creates suitable ecological conditions to play an essential role in the transmission of the larvae of tapeworms. The large number of cysts of *N. singularis* (above 80 found) and their great vitality indicate that this representative of *Catops* sp. was a host in which the larvae found suitable living conditions.

Necrophorus vespilloides (Herbst)

This species is a necrophagous organisms. Out of 161 examined specimens, in one of them over 100 cysts of the cysticercoïd type (Fig. 5a, b) were found, which could be identified with any of the tapeworms parasitizing micro-mammals.

Silpha (Thanatophilus) sinuata Fabr.

It is a necrophagous species. In 33 examined individuals, one proved to be a carrier of unknown larvae of the cysticercoïd type (Fig. 5c, d).

2. Final host (*S. araneus araneus*), its biology and state of invasion with parasites

According to Borowski et Dehnel 1952 the span of life of *S. araneus araneus* lasts several months to over one year. Independently of the span of life of separate individuals it can be stated that one generation of the common shrew lives more or less about 18 months.

The common shrews born in the first litter leave the nests at the beginning of June. Starting from this time the population of the common shrew is composed during the whole summer-autumn season of: mature individuals born in the previous year which survived the winter, and young animals born in a current year. The females are able to have several litters in a season and even in September pregnant females or lactating females (Tarkowski 1957) can be found. Thus the young shrews are of various age (one, two or three-month-old), depending on the litter from which they originate.

By the end of summer and in autumn the overwintered shrews and certain percentage of the young ones gradually die out. The young animals which survive winter attain the maturity in March of the next year, what is a sudden and simultaneous phenomenon (Tarkowski 1957). The reproduction season (the first oestrus) begins in April, and the first litters appear in May. The appearance of the first young shrews (juv) and of those which survived winter (ad) in the separate months of the year is illustrated in Table VI.

Table VI
Occurrence of young (juv.) and old (ad.) common shrews throughout the year
(after Borowski et Dehnel)

S h r e w s	M o n t h												
	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI
Old (overwintered)	ad.	ad.	ad.	ad.	ad.	-	-	-	-	ad.	ad.	ad.	ad.
Young	juv.	juv.	juv.	juv.	juv.	juv.	juv.	juv.	juv.	-	-	-	juv.

Out of 2030 shrews examined, 1710 were invaded with various species of tapeworms. The extensiveness of invasion in the whole material is 83.9%. This number indicates a very high invasion, it does not reflect, however, certain regularities and variabilities in the degree of invasion of shrews in various periods of their life and in various seasons of the year. To reflect this, the material was segregated into separate years and months and the data for young and overwintered shrews are given separately (Table VII).

T a b l e VII
Invasion of young (juv.) and old (ad.) common shrews in various months of the year

Year	Age	January			February			March			April			May		
		Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%
1953	ad.	-	-	-	-	-	-	-	-	-	-	-	-	16	9	56.2
	juv.	-	-	-	-	-	-	-	-	-	-	-	-	14	7	50.0
1954	ad.	-	-	-	x	x	x	10	5	50.0	32	14	43.7	32	27	84.3
	juv.	-	-	-	7	3	42.8	x	x	x	x	x	x	x	x	x
1955	ad.	x	x	x	x	x	x	28	24	85.7	26	25	96.1	4	3	
	juv.	27	17	62.8	21	12	57.1	x	x	x	x	x	x	x	x	x
1956	ad.	x	x	x	x	x	x	26	25	96.1	23	23	100.0	-	-	-
	juv.	19	10	52.6	8	2	25.0	x	x	x	x	x	x	x	x	x
1957	ad.	x	x	x	x	x	x	7	6	85.7	8	7	87.5	9	9	100.0
	juv.	13	9	69.2	12	8	66.7	x	x	x	x	x	x	x	x	x
1958	ad.	x	x	x	x	x	x	6	5	83.3	17	17	100.0	3	3	
	juv.	14	9	64.4	9	7	77.8	x	x	x	x	x	x	x	x	x
1959	ad.	x	x	x	x	x	x	3	3		5	5	100.0	1	1	
	juv.	8	8	100.0	5	5	100.0	x	x	x	x	x	x	x	x	x

continuation; horizontal rubrics as above

June			July			August			September			October			Nov. and Dec.		
Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%	Exam.	Inv.	%
12	10	83.3	11	11	100.0	55	54	98.1	36	36	100.0	15	15	100.0	1	1	
39	30	76.9	91	86	97.8	135	129	94.8	67	64	95.5	17	16	94.1	20	12	60.0
9	6	66.7	22	19	86.3	32	30	93.7	48	46	95.1	15	14	93.3	3	2	
34	24	70.6	145	102	70.3	160	121	75.6	64	47	73.4	22	18	81.8	34	24	70.6
41	32	78.0	5	4	80.0	15	15	100.0	7	7	100.0	2	2		x	x	x
42	32	76.2	41	36	87.8	51	49	96.0	11	11	100.0	2	2		20	16	80.0
12	10	83.3	5	5	100.0	2	2		1	1		5	5	100.0	2	2	
8	7	87.5	6	6	100.0	6	6	100.0	1	1		7	6	85.7	14	12	85.6
6	6	100.0	5	5	100.0	8	8	100.0	3	3		12	11	91.6	1	1	
10	9	90.0	15	14	93.2	18	18	100.0	1	1		7	7	100.0	18	17	94.4
1	1		7	7	100.0	7	7	100.0	3	3		1	1		x	x	x
10	9	90.0	18	17	94.4	34	32	94.1	12	12	100.0	14	14	100.0	13	13	100.0
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

- lack of data; x lack of a given age group

Extensiveness of invasion

The data in Table VII served to make the diagram which illustrates the variability of invasion of the successive generations of shrews in 1953—1958 (Diagram 1). This diagram shows the state of infestation of the successive generations of the common shrew in the separate months of the year as well as the differences in the infestation of two simultaneously existing generations (parents and offspring). Diagram 2 shows even more markedly the relations in all the years jointly.

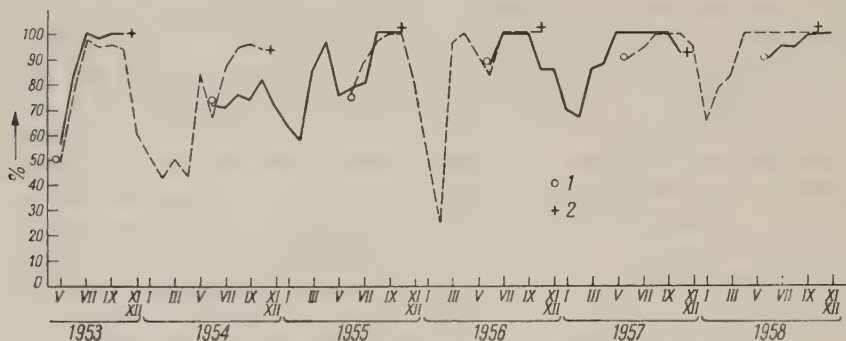


Diagram 1. Invasion of successive generations of a common shrew with tapeworms in separate months in 1953—1958

1 — occurrence of a new population, 2 — dying out of an old population



Diagram 2. Differences in degree of invasion with tapeworms of two parallelly living generations of a common shrew (parental and descendent)

1 — young animals, 2 — overwintered animals

From these diagrams two basic and repeating regularities result: (1) In every generation the state of invasion attains twice its maximum and once its minimum. The first maximum concerns young shrews, born in a given year, and appears most commonly in August and September, the second one in summer (June, July, August) and concerns the overwintered individuals. The decrease of the extensiveness begins late in autumn or at the beginning of

winter and attains its minimum most commonly in February; (2) The extensiveness of invasion of young shrews, particularly in summer, is on the whole lower than in the parental generation living parallelly.

The explanation of these regularities can be found in the biology of the final and intermediate hosts, and in the influence of the year season on the kind of food and way of life of those hosts.

The young shrews, which remain in nests three weeks after the birth, are fed with mother's milk and most likely have no intestinal parasites. When they start their active life outside nests they change to animal food composed of various small invertebrates (e. g., insects, snails, myriapods), which are the intermediate hosts of tapeworms. The shrews have a quick metabolic rate and must feed themselves intensively. According to Tupikova 1949, the daily rations of the ingested food surpass oftentimes their body weight. Because every tenth insect, myriapod, or snail, is infected with the larvae of tapeworms, it can be assumed theoretically that the shrews just after the first day outside the nest can already become infected at least with one species of tapeworm. This can be corroborated by the fact that already in the animals collected at the beginning of June the extensiveness of invasion is relatively high (Diagram 1).

In summer and early autumn, that is at the time of the active appearance of all the hitherto known intermediate hosts which form the food of the shrew, there is a permanent possibility for these animals to get invaded with tapeworms. Therefore the percentage of the invaded shrews rises and attains a certain maximum in summer or at the beginning of autumn.

In the late autumn the invertebrates hide for winter and become scarcely accessible to the shrews. The shrews are in a state of winter vegetation and abstain from seeking food, hence they have no chance to get invaded. They change, at least partly, to plant food. The animal food discovered by them at that time differs qualitatively from that available in summer, when the abundance of invertebrates permitted to make a certain selection.

With the disappearance of invertebrates, a very important link in the developmental cycle of tapeworms disappears too. The shrews, remaining on a quantitatively limited and different animal food, become not invaded to such a degree as in summer. This concerns at least the majority of the species of the parasites.

As shown by observations, shrews kept on a diet under breeding conditions lost after several months the tapeworms acquired in the field (Kisielewska 1960a). This may be explained by the limited span of life of the tapeworms which after death are removed from the alimentary tract of the shrew. It cannot be excluded that this mortality is accelerated by the special diet used under breeding conditions, because this diet is not typical to the animals living under field conditions. The limitation of secondary invasion and the different diet are also characteristic under natural conditions in winter and most likely this is the cause of the winter depression in the extensiveness of invasion of shrews at that time.

The onset of spring causes a new appearance of intermediate hosts and the overwintered shrews, which became partly free of worms in winter, begin to renew their tapeworms. This is the reason of the second maximum invasion in the same generation of shrews.

The fact that the young shrews are less invaded than the old ones and that they attain their maximum invasion later, can be explained in the following way. According to Tarkowski 1957, the females are able to have several litters in a season. Thus the population of young shrews which led already for a certain time the outside-nest life and became invaded with tapeworms is constantly joined by young individuals from later litters, the invasion of which at the moment of leaving the nest equals practically to zero. Therefore the extensiveness of invasion in all young shrews (with no consideration of age groups) is relatively lower than in older ones.

Intensity of invasion

The intensity of invasion with *Staphylocystis furcata*, *Soricinia tripartita* and *Dilepididae* sp. is up to 20 specimens, with *Vigisolepis spinulosa* and *Hymenolepis* (s. l.) *scutigera* up to 50—60, with *Soricinia diaphana*, *Neoskrjabinolepis singularis* and *Choanotaenia crassiscolex* up to 100—150, and with *Pseudodiorchis prolifer* several thousand to over ten thousand specimens in one host.

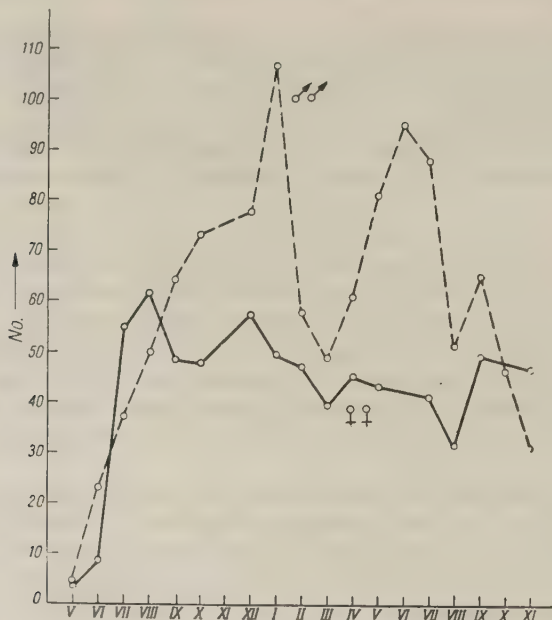


Diagram 3. Differences in the mean intensity of invasion with tapeworms of males and females of a common shrew

The Diagram 3 illustrates the average intensivity of invasion of males and females in the separate months, calculated jointly for all the examined generations. *Pseudodiorchis prolifer* was omitted in this diagram because it occurred relatively seldom (the extensiveness for the whole material is 19.3%); if this species were included the mean intensivity would increase very considerably and thus would not reflect the actual state of the invasion.

The diagram indicates that the intensivity of invasion of males is as a rule higher than that of females. It seems to me that this phenomenon may be explained, at least partly, as to the overwintered shrews. From April (the beginning of the reproduction season in shrews) till September the overwintered males search after females and therefore show a great activity (Borowski et Dehnel 1952). This increases their food requirements and creates greater chances to meet various invertebrates. However, the overwintered females prepare nests and feed the offspring, therefore their activity is considerably lower than that of males. These differences in activity effect most likely the frequency of secondary invasion of males and females.

Borowski et Dehnel 1952 assume that the activity of young, immature males and females is the same. In spite of that, the diagram 2 shows that the intensivity of invasion of males is considerably higher than that of females. This fact proves that the phenomenon of the more intensive infection of males than females cannot be explained solely by the difference of activity of both sex groups.

3. Dynamics of circulation of tapeworms of *S. araneus araneus* in the BNP

(a) Circulation of individual species of tapeworms

So far the data concerning the extensiveness of invasion included cestodofauna as a whole. However, it seems to be purposeful to review the state of invasion with every species of tapeworm individually, because on the basis of their life cycle described so far it was proved that (1) in the circulation of those parasites in BNP the representatives of three groups of invertebrates take part, among them at least three species of insects, one species of myriapods and eleven species of terrestrial snails, (2) each of this species or group of species is characterized by certain distinct properties as regards the period of active life in the field and its abodes, (3) each of them constitutes most likely the food of various value to the shrews.

The data will concern all the years jointly. The calculations were made exclusively in relation to the invaded individuals to show more distinctly the differences in the degree of invasion of shrews with the individual species of tapeworms.

Soricinia diaphana and *Staphylocystis furcata* pass in their development through the coprophagous insect *Geotrupes stercorosus*. The Diagram 4 illustrates the state of invasion of the common shrew with those species. The course of the two curves, although at the various levels, is more or less similar. It is an evidence of the following phenomena: (a) *Soricinia diaphana* occurs considerably more commonly than *St. furcata*. As shown in the Table V, the extensiveness of both tapeworms species is almost the same, and even a little higher for *St. furcata*. Therefore it seems that *Soricinia diaphana* possesses in the BNP a second, not yet known, intermediate host, which constitutes a more common food; (b) The highest invasion with both tapeworm species of young and overwintered animals falls on late summer, autumn and the beginning of winter. It is most likely connected with the fact that in July and August there is the highest invasion of *Geotrupes stercorosus* with the larvae of those tapeworms (Table V); (c) The greatest decrease of invasion is recorded in

April and May, i.e., in the months preceding the spring appearance of *G. stercorosus* in the biocenosis after the winter vegetation (Borowski 1960).

The variability of invasion with both tapeworm species shown in the Diagram 3 is confirmed by the dissections of shrews. In July, August and September in the alimentary tract of the shrews there were found young tapeworms, at the scolex stage or in the beginning of strobilization. I did not find such forms in winter, although it can not be excluded that sporadic cases of invasion took place in this period.

The life cycle of *Neoskrjabinolepis singularis* has not been in detail described. It was only found (Kisielewska 1958b) that an insect of the genus *Catops* is one of the intermediate hosts.

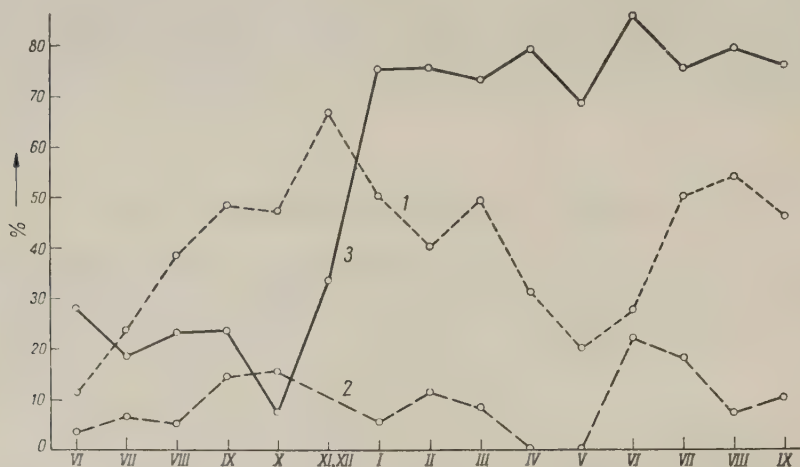


Diagram 4. Variability in the degree of invasion of a common shrew (ad. and juv.) with *Staphylocystis furcata*, *Soricinia diaphana*, and *Neoskrjabinolepis singularis*
1 — *Soricinia diaphana*, 2 — *Staphylocystis furcata*, 3 — *Neoskrjabinolepis singularis*

The Diagram 4 illustrates the variability of invasion with this tapeworm species also. The curve runs here completely differently than in the case of the previously described species. It shall be mentioned that *N. singularis* occurs frequently in the common shrew, that the young animals are considerably less invaded than the overwintered ones, and that a significant increase of invasion is observed in winter, what is also confirmed at postmortems (from December till April there were found numerous young forms, what indicates a secondary invasion).

In view of inaccurate informations on the life cycle of *N. singularis* it is difficult to explain the previously cited regularities. However, the biology of the insect, the intermediate host, seems to explain a great deal. *Catopidae* live in the nests of birds and mammals where they undergo the whole metamorphosis. It can be supposed that, as the insects living in nests, they are in winter easier accessible as food to the shrews than other insects overwintering in the ground or under bedding. If this point of view is accepted, the significant increase of invasion with this tapeworm at the beginning of winter, and

the presence of its numerous young forms in the alimentary tract of the shrew in winter and spring become clear. This hypothesis should be confirmed by accurate informations on the life cycle of *N. singularis* and on the qualitative food composition of the shrew in the various periods of year.

Various terrestrial snails are the intermediate hosts of *Ch. crassiscolex* (Table IV). The variability of invasion is illustrated in the Diagram 5 which indicates that in spring, summer and autumn the state of invasion of both the young and the overwintered shrews is very high. Young forms of this tapeworm are

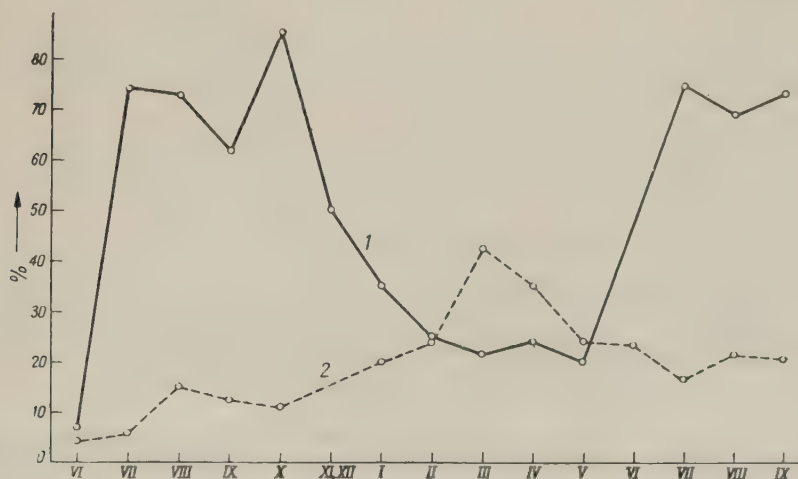


Diagram 5. Variability in the degree of invasion of a common shrew (ad. and juv.) with *Choanotaenia crassiscolex* and *Pseudodiorchis prolifer*
1 — *Choanotaenia crassiscolex*, 2 — *Pseudodiorchis prolifer*

found in shrews and larvae in the snails during this whole period. In winter no dissections of snails were made, but the sporadic occurrence of this tapeworm at the scolex stage proves that the overwintered snails possess also the invasive cysticercoids of *Ch. crassiscolex*.

Pseudodiorchis prolifer passes in its developmental cycle through the myriapod, *Glomeris connexa*. Diagram 5 indicates that the level of invasion is rather uniform with the exception of winter, when a certain increase of the invasion is marked. Discussing the biology of the intermediate hosts it was mentioned that *G. connexa* lived mainly in decaying trunks of trees. It can be supposed that they are easily accessible to the shrews during the whole year. The shrews, however, reluctantly take food from the trunks in spring and summer, when there is plenty of food on the surface. It is not before the famish winter period that compels them to seek such a food.

The Diagram 6 illustrates the state of invasion of shrews with two tapeworm species, the intermediate hosts of which are completely unknown. The curve illustrating the extensiveness of invasion with *Vigisolepis spinuosa* does not show any significant regularity.

In the case of *Hymenolepis* (s. l.) *scutigera*, May and June are characterized by an increase of invasion, contrary to the uniform, low level during the

remaining months. Any attempt to explain the course of the curves seems to be premature in view of the lack of information concerning the routes of the circulation of the tapeworms in the biocenosis. Only as regards *H. scutigera* it can be supposed that its intermediate host is some invertebrate which appears in great masses and in a short period of time (in spring).

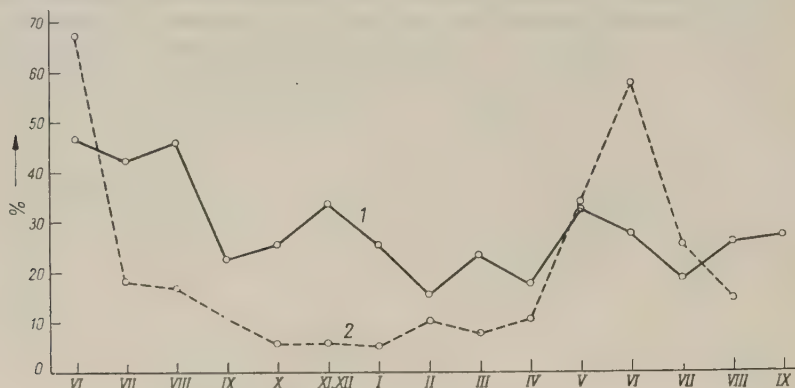


Diagram 6. Variability in the degree of invasion of a common shrew (ad. and juv.) with *Vigisolepis spinulosa* and *Hymenolepis* (s. l.) *scutigera*
1 — *Vigisolepis spinulosa*, 2 — *Hymenolepis* (s. l.) *scutigera*

Soricinia tripartita and the young forms of *Dilepididae* sp. are also characterized by unknown life cycles. The first of them was found in July (4.2% of extensiveness), August (7.1%), September (9.2%), October (9.1%); in 1957 it was found also in January (10.2%) and February (11.1%). *Dilepididae* were found exclusively in July (5.7%), August (10.0%) and September (1.4%).

(b) Variability of the numerosity of the coexisting species

One, two, three, four or more tapeworm species were found in the individual shrews in the BNP. The observations proved that the number of the coexisting species is not accidental, but depends on the year season, because every season creates different conditions for the circulation of tapeworms in the biocenosis. The data are illustrated in the Table VIII, and the graphic representation can be seen in the Diagram 7.

The Table VIII and the Diagram 7 reflect the following observations: (1) in June in the majority of young shrews one tapeworm species was found. Most likely these animals were searching for food for a short time (they left the nests recently) and did not have the chance to enrich their tapeworm fauna; (2) from July till September the number of the shrews invaded with 2, 3, 4, and 5 tapeworm species increases. This phenomenon appears both in young and in overwintered animals. This is connected with the active occurrence of the majority of invertebrates, and with the constant possibility of the secondary invasions; (3) in October the percentage of shrews invaded with one tapeworm species rises again both in young and overwintered animals. One of the reasons of this phenomenon is undoubtedly the fact that certain tapeworm species die in autumn and a partly spontaneous liberation of the final

hosts from the worms occurs. However, the analysis of tapeworm species which pass the winter (seven of ten known) in the animals induces to a different interpretation of the disappearance of the multi-species ensembles in autumn. As known from the literature (Borowski et Dehnel 1952, Dehnel 1949), the overwintered animals and some percentage of young

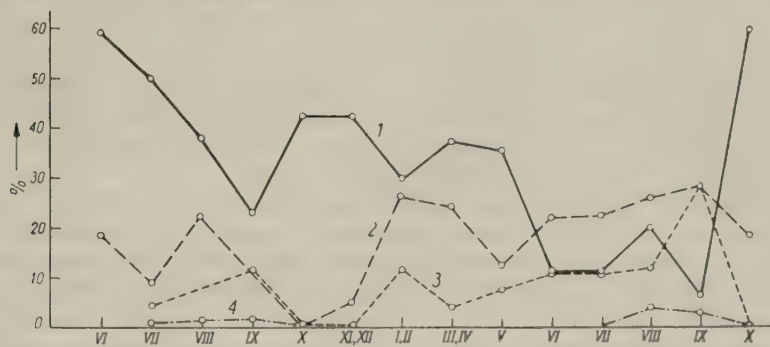


Diagram 7. Occurrence of monospecific and polyspecific tapeworm ensembles in separate months of the year in a common shrew (ad. and juv.)

1 — monospecific ensembles, 2 — three-specific ensembles, 3 — four-specific ensembles, 4 — five-specific ensembles

Table VIII

Percentage of young (juv.) and old (ad.) common shrews invaded with various number of tapeworm species

No. of tapeworm species	June		July		August		September		October		Nov., Dec.		Jan., Feb.		Mar., Apr.		May	
	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.
one	59.4	11.1	50.0	11.1	37.8	20.0	25.9	6.3	42.8	60.0	42.3	x	29.9	x	x	37.6	x	35.7
two	21.9	55.5	35.4	55.5	29.9	36.0	50.0	34.4	57.2	20.0	52.4	x	32.0	x	x	34.0	x	53.9
three	18.7	22.2	9.3	22.2	22.1	26.0	11.1	28.1	-	19.0	5.3	x	26.4	x	x	24.4	x	12.8
four	-	11.1	4.7	11.1	7.9	12.0	11.2	28.1	-	1.0	-	x	11.7	x	x	4.0	x	7.6
five	-	-	0.6	-	1.6	4.0	1.8	3.1	-	-	-	x	-	x	x	-	x	-
six	-	-	-	-	0.7	2.0	-	-	-	-	-	x	-	x	x	-	x	-

x - lack of a given age group

shrews die out in autumn (the so called autumnal death of the shrews). Borowski et Dehnel 1952 put a hypothesis that the parasites are one of the factors regulating the quantitative state of shrews in the field. The above mentioned phenomenon of the autumnal disappearance of the multi-species ensembles of tapeworms seems to confirm that hypothesis, because in autumn first of all die out those animals which were infected simultaneously with several tapeworm species; (4) Already in December there start to appear again

in the overwintered shrews three and four-species ensembles of tapeworms. This is most likely connected with the fact that the shrews become invaded with certain tapeworm species (e. g. *Neoskrjabinolepis singularis*, *Pseudodiorchis prolifer*) also in winter.

(c) Variability of the quantitative composition of tapeworms and domination of individual tapeworm species

The extensiveness of invasion of all examined shrews (2030 individuals) with the separate tapeworm species was as follows: *Neoskrjabinolepis singularis* 56.4%, *Choanotaenia crassiscolex* 51.4%, *Soricinia diaphana* 46.8%, *Vigisolepis spinulosa* 28.3%, *H. (s. l.) scutigera* 20.7%, *P. prolifer* 19.3%, *S. furcata* 8.4%, *S. tripartita* 2.7%, and *Dilepididae* sp. 2.1%.

The reasons of the different extensiveness of invasion should be found most likely in the link of the development of the parasites, connected with the intermediate hosts. Presumably the numerical state of any tapeworm species in a given biocenosis depends to a considerable degree on the fact, whether its intermediate hosts occur in great numbers in a proper season of their activity, and whether they are one of the fundamental constituents of food of the shrews.

The Diagram 4, 5, 6 indicate, however, that it is impossible to speak of a domination of any tapeworm species in the absolute sense without taking into consideration its variability in the various year seasons and in the various periods of life of the final host.

As it was already stressed, in June the young shrews are invaded mainly with only one tapeworm species (Diagram 7). Among the mono-species ensembles the leading place is occupied to a considerable degree (57.9%) by *Hymenolepis scutigera*. The parasite appears also in the compositions of the bi-species ensembles (86.2%) and three-species ensembles (100.0%). This is in accordance with the Diagram 6 which indicates that in June there is a high percentage of invasion with this species among young shrews.

The second species, as regards the frequency of occurrence, is *Vigisolepis spinulosa*: 26.3% of the mono-species ensembles, 62.5% of the bi-species ensembles (with *Hymenolepis scutigera*), 100.0% of three-species ensembles (with *H. scutigera* and some third species). The other species occur singularly in an insignificant percentage (jointly 15.8%). The intermediate hosts of those tapeworms lead already at this time an active life in the field. The occurrence of those species in young shrews so rarely throws interesting light on the selectiveness of food of these animals directly after leaving the nest.

It is almost exceptional to find in July mono-species ensembles in which *H. scutigera* would be found (barely 12.6%). It enters the multi-species ensembles because the shrews managed already to enrich since June their cestodofauna acquiring two, three, or more species. Young *H. scutigera* are found in the mentioned month only sporadically what is a proof that the invasion with this species became considerably hindered. The frequency of occurrence of this species drops to several per cent and on this level it will remain till June of the next year, when it will occur again for a short time in great numbers as the seasonal dominating species, but this time in the overwintered animals (Diagram 6). In July there is a rapid increase of invasion with *Ch. crassiscolex*

which occurs singularly in 36.7%, in bi-species ensembles in 88.0%, in three-species ensembles in 75.1%, and in four-species ensembles in 52.0%. An expression of the rapid invasion of this species are also the data shown in the Diagram 5. The second, as to the frequency of occurrence, is *S. diaphana* (increase of extensiveness of invasion in relation to June). *Vigisolepis spinulosa* and *Neoskrjabinolepis singularis* remain more or less on the same level in June. Besides, there appear species hitherto not observed: *S. tripartita* and *Dilepididae* sp. This state is maintained throughout August and September.

In October, November and December, when the cestodofauna becomes quantitatively poor, exclusively mono- and bi-species ensembles were found, and *S. tripartita* and *Dilepididae* sp. were completely absent. Although the remaining species occur less frequently, they preserve the numerical proportions of the summer season (the most numerous: *Ch. crassiscolex*, *S. diaphana*, *V. spinulosa*).

In January and February the tapeworm fauna is renovated, and the shrews become invaded with *Neoskrjabinolepis singularis* and *Pseudodiorchis prolifer* (Diagram 4 and 5). *N. singularis* occurs in mono-species ensembles in 72.3%, and in bi- and three-species ensembles in 100%. This species retains its dominating position in the overwintered animals till the end of their life.

In June, in the overwintered shrews there occurs again for a short time *Hymenolepis scutigera*, in July increases the invasion with *Ch. crassiscolex*, and again *S. tripartita* and *Dilepididae* sp. occur. The enrichment of the tapeworm fauna runs in summer in the overwintered animals similarly as in young ones. In October and November there occur exclusively *N. singularis*, *Ch. crassiscolex*, *S. diaphana* and *Vigisolepis spinulosa* in mono- or bi-species ensembles.

(d) Analysis of the reasons of dynamics of the tapeworms circulation

Analysing the reasons of the variability of the degree of intensivity of the circulation of tapeworms in the BNP biocenosis it is possible to discern two groups of factors: decisive factors which bestow to the dynamics a general, every year repeated character, and modifying factors which act only once, occasionally.

The first of the decisive factors is the phenological one, a season of the year. It does not seem that it acts directly on the tapeworms, but it exerts a clear influence both on the intermediate and on the final hosts. They influence on the seasonal activity (spring, summer) or vegetation (winter) of invertebrates and common shrews, to which spring and summer are the seasons of increased activity („araneus season” — Borowski et Dehnel 1952), contrary to winter, when a major activity is shown by *Sorex minutus* L. („minutus season”). The phenological factor has also an indirect influence on the quality of food taken by mammals and invertebrates. Thus, the seasons of the year decide that the circulation of the majority of tapeworm species is in winter completely impossible, or at least considerably limited, and in summer is very intensive. This is the course of the curves (Diagram 1 and 2) which show these repeating regularities in the successive generations of shrew in spite of various years and quantitatively various material.

The curves in Diagram 4 and 5 illustrating the invasion of shrews with the individual tapeworm species of the known life cycle, express the influence of biology and mode of life (the second decisive factor) on the concrete intermediate hosts.

In the case of *Soricinia diaphana*, *Staphylocystis furcata*, and *Choanotaenia crassiscolex* the curves of the extensiveness take a course (Diagrams 4 and 5) similar to that in the Diagram 1. Most likely this results from the fact that the mode of living of the intermediate hosts of these tapeworms is strictly dependent on the season of the year. In the case of *Neoskrjabinolepis singularis* and *Pseudodiorchis prolifer* the curves of the extensiveness take a different course. This is most likely caused by the fact that their intermediate hosts lived in nests and tree-trunks also in winter and therefore became less dependent on the climatic seasonal changes.

A modifying factor can be some unfavourable period in which the occurrence of some invertebrate species becomes depressed. This will result undoubtedly in some disturbances in the circulation of the tapeworm species to which the invertebrate animal is an intermediate host. The climatic conditions can also be the modifying factors. Thus, the long rainfalls which lower the activity of insects and cause a massive appearance of snails will certainly have an influence on the intensivity and rate of the circulation of tapeworms. An early spring or a late winter, preceded by a warm and fair autumn, may extend the period of activity of invertebrates, and this automatically extends the time of the circulation of tapeworms in the biocenosis. Many such examples can be here cited. However, on the basis of several years, in which the material analysed in the present work was collected it can be supposed that these factors do exert not such a big influence to be able to disturb the general character of invasion of shrews with tapeworms.

Serious disturbances, or even a disappearance of certain tapeworm species in the biocenosis of the BNP, may occur in 1960. It was a catastrophic year as regards the shrews, because it was almost impossible to collect them. The rainy summer could not be blamed for causing it, because the rain rather increases the activity of shrews (Borowski et Dehnel 1952). Therefore it should be concluded that simply there was an absence of those mammals in the field. On the other hand the rain lowers considerably the activity of insects. The almost complete absence of shrews and the considerably decreased activity of insects caused that some tapeworm species seem to be in a great danger. The subsequent years will show to what an extent this supposition is correct.

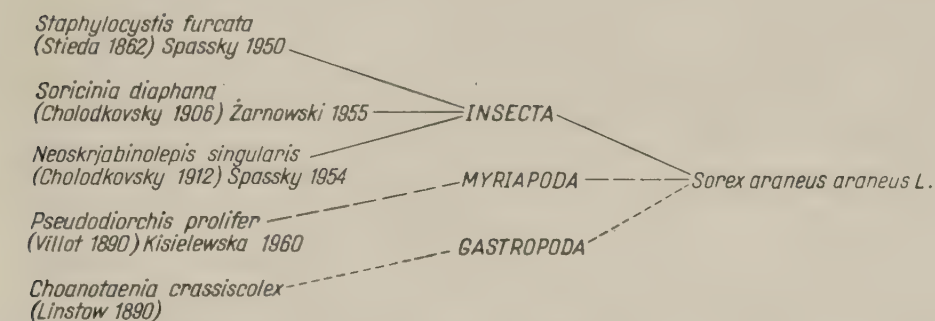
4. Routes of circulation of tapeworms of the common shrew in the BNP biocenosis

The wholeness of the phenomena and processes connected with the life cycle of tapeworms are defined by me as the circulation of parasites in the biocenosis, after Wiśniewski (1955, 1958) and his coworkers (Jarecka 1958, Rybicka 1958, Sulgostowska 1958, and others).

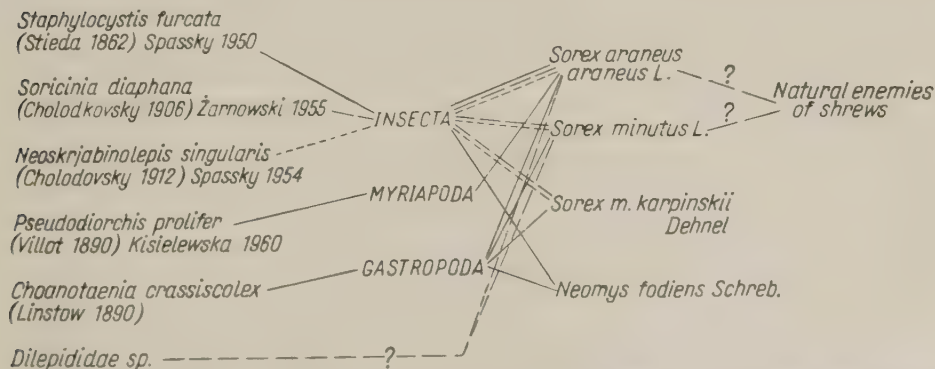
The circulation of parasites is conditioned by certain factors (1) the composition of the biocenosis must include the proper final host — the environment of the sexual reproduction of the adult forms of tapeworms, and the

intermediate hosts — in which the stage of the ontogenesis from the oncosphere to the cysticeroid takes place; (2) the occurrence of the intermediate hosts and final hosts must be simultaneous, at least in a certain period of time, and their field expansion should be totally or partly the same; (3) between the intermediate and the final host there must be an ecological connection, an alimentary chain, proper to the given biocenosis. This means that the intermediate host must form a proper, natural, not accidental food to the final host; (4) the mode of living, the way of taking food, the quality of food, and the places of occurrence of the intermediate host must create a permanent, or periodical, but not an accidental chance for the contact with the eggs of parasites. The simultaneous coexistence of the proper species of intermediate and final hosts decide the possibility of repeated closing of the life cycles in tapeworms, that is their circulation in the biocenosis.

On the basis of the hitherto examined life cycles of tapeworms parasitizing common shrew in the BNP it is possible to discern three routes of circulation of these parasites: (a) through myriapods, (b) through snails, (c) through insects (Scheme A).



Scheme A. Circulation ways of tapeworms, parasites of a common shrew in the biocenosis of Białowieża National Park



Scheme B. Circulation ways of tapeworms, parasites of a common shrew and some other *Soricidae* in Białowieża National Park

This scheme can be supplemented by the Solty's 1954 data concerning the invasion of other *Soricidae* in the BNP, which were not examined by me (Scheme B, Table IX). The data are here certainly not complete, but have some value, because they signalize the possibility of the occurrence of a given tapeworm species in a given mammal species, i. e. the existence of the established route of circulation.

T a b l e I X
Invasion of other *Soricidae* species with tapeworms occurring
in *Sorex araneus araneus* in BNP (after Solty's 1954)

Tapeworm species	Sorex minutus (749 examined)		Sorex macropygmaeus karpiński (50 examined)		Neomys fodiens (288 examined)	
	Invad.	%	Invad.	%	Invad.	%
<i>Choanotaenia crassiscolex</i>	1	0.1	3	6.0	1	0.3
<i>Soricinia diaphana</i>	11	1.4	2	4.0	0	0
<i>Hymenolepis singularis</i> (-Neoskrjabinolepis singularis)	6	0.7	4	8.0	0	0
<i>Dicranotaenia furcata</i> (-Staphylocystis furcata)	0	0	0	0	1	0.3

Out of nine tapeworm species found in *S. araneus araneus* in the BNP, the life cycles of five were examined. It cannot be stated with certainty that the detected intermediate hosts are the only ones for the given tapeworm species in the Białowieża biocenosis. Moreover, in other *Soricidae* there occurs a number of tapeworm species not observed in the common shrew, the developmental cycles of which are unknown. As an example can serve tapeworms of *Neomys fodiens*, the cysticeroids of which were found by Prokopič (in litteris) in Czechoslovakia in *Gammarus pulex*. Thus, the described routes of circulation do not exhaust all the possibilities existing in the BNP biocenosis; they illustrate only the present state of the conducted studies. I do not mention even those tapeworm species to which the common shrew and other small mammals serve as intermediate hosts.

Wiśniewski 1955, 1958 on the basis of the work of Jarecka 1958 differentiated at the lake Družno two ways of the circulation of tapeworms of birds (*Anatinae* and *Fulica atra*). Their cycle requires one intermediate host: (1) plankton (*Copepoda*, *Ostracoda*, *Cladocera*) — 18 cysticeroid species, and (2) snails (*Pulmonata*) — 2 cysticeroid species.

Comparing the routes of the circulation of the tapeworms of water birds of the lake Družno and those of the insectivorous mammals in the BNP, in spite of the diametrically different environments (water — earth) and the belonging of the final hosts to the different classes, it is possible to notice certain common characteristics. And so: (a) both the lake Družno and the BNP are envi-

ronments trophically rich, therefore numerous inhabited by various species of invertebrates and vertebrates. This creates for the parasites great possibilities as regards the routes of circulation; (b) in both biocenoses the tapeworms in their ontogenetical development use the existing connections of the alimentary chain between the intermediate and final hosts; (c) both in the water and in the land environment there is a phenomenon of the focal invasion with cysticeroids of the invertebrates of poor movements: plankton crustaceans and snails in Družno (Wiśniewski 1955, 1958, Jarecka 1958), and myriapods and snails in BNP; (d) vertebrates proved to be first of all the final hosts, to a considerably smaller degree the intermediate hosts.

5. Specificity of tapeworms parasitizing *Soricidae* in the BNP

In the BNP the following species of *Soricidae* were found (Borowski et Dehnel 1952): *S. araneus araneus* L., *S. minutus* L., *S. macropygmaeus karpinskii* Dehnel, *Neomys fodiens* Schreb., *N. anomalus milleri* Mott.

The authoress' data on the tapeworms of the common shrew and Solty's (1954) data dealing with the remaining species of *Soricidae* indicate that in those animals 13 species of tapeworms (Table X) occur.

Table X
Occurrence of tapeworm species in the representatives of *Soricidae*
(Nomenclature after Solty's 1954, except of tapeworms of *S.a.araneus*)

Tapeworm species	Mammalian species				
	<i>S.araneus araneus</i>	<i>S.minutus</i>	<i>S.macr. karp.</i>	<i>Neomys fodiens</i>	<i>N.anom. milleri</i>
<i>Stapyllocystis furcata</i>	+	-	-	+	-
<i>Neoskrjabinolepis singularis</i>	+	+	+	-	-
<i>Soricinia diaphana</i>	+	+	+	-	-
<i>Soricinia tripartita</i>	+	-	-	-	-
<i>Pseudodiorchis prolifer</i>	+	-	-	-	-
<i>Vigisolepis spinulosa</i>	+	+	+	-	-
<i>Hymenolepis (s.l.) scutigera</i>	+	-	-	-	-
<i>Dicranotaenia soricis</i>	-	-	+	-	-
<i>Choanotaenia crassiscoler</i>	+	+	+	+	-
<i>Dicranotaenia globosoides</i>	-	+	-	+	+
<i>Hymenolepis tridentophora</i>	-	-	-	+	-
<i>Hymenolepis magnirostellata</i> f.44	-	-	-	+	+
<i>Hymenolepis anacetabulata</i>	-	-	-	+	+

Table X shows that the tapeworm species occurring in *Soricidae* can be subdivided into three groups: (1) typical (specific) species to the representatives of the genus *Sorex*; (2) typical (specific) species to the representatives of the genus *Necmys*, and (3) species occurring in these two genera.

It seems to me that this specificity is connected to a large degree with the areas of the occurrence of mammals and invertebrates, being intermediate hosts of tapeworms.

The species of the genus *Sorex* are typically terrestrial, although *S. minutus* prefers more humid terrains than does *S. araneus araneus* and *S. macro-pygmaeus karpiński*. They search for food on the surface of the bedding, in the bedding, in tree-trunks and under tree-bark. Their main food are the terrestrial invertebrates.

The representatives of the genus *Neomys* lead a terrestrial-aquatic mode of living. They inhabit exclusively humid biotopes, keep close to the aquatic reservoirs, and search for food under water; their main food constitutes of aquatic invertebrates (crustaceans, insects and larvae of insects developing in water — Dehnel 1950, Borowski et Dehnel 1952).

The hitherto known intermediate hosts of tapeworms typical to the genus *Sorex* are terrestrial insects and myriapods living in dry biotopes. It seems therefore clear that species of the genus *Neomys*, living in biotopes distinctly humid and taking their food in water, can not be infected with tapeworms developing in those invertebrates.

In *Neomys fodiens* Sołtys 1954 found sporadically *Staphylocystis furcata*, a tapeworm typical to the genus *Sorex*. Dehnel 1950, and Borowski et Dehnel 1952 report that *N. fodiens* enlarges in summer its living area and penetrates into biotopes somewhat more distant from the water. During these migrations single individuals of this mammal could come in touch with a terrestrial invertebrate, which is the intermediate host of *S. furcata*. This seems to indicate that the specificity of certain tapeworm species to the hosts of the genus *Sorex* has rather an ecological character than a physiological one.

In the BNP the developmental cycles of the tapeworms occurring in the genus *Neomys* were so far not yet studied. However, Prokopič in Czechoslovakia (in litteris) found the cysticercoids of these tapeworms in *Gammarus pulex* (Crustacea). These crustaceans, if any, occur in the rivers of the BNP in evenescent numbers. It seems, however, probable that this or some other, more common species of an aquatic invertebrate, serves as an intermediate host of the majority of tapeworms of *N. fodiens* and *N. anomalus milleri*. This, in turn, would explain why the representatives of the genus *Sorex* living far from water do not become invaded with tapeworms typical to the genus *Neomys*. The example of *Dicranotaenia globosoides* Sołtys 1954 proves that also in this case the exclusiveness is dependent on the ecological conditions, because this parasite occurs in both species of the genus *Neomys* and in *Sorex minutus* (Sołtys 1954). As already mentioned, *S. minutus*, although a typical terrestrial animal, likes humid biotopes where also the representatives of the genus *Neomys* are living. On the terrain jointly inhabited it has the possibility to become infected with the same form of the parasite as the species of the genus *Neomys*. It should be supposed, however, that the intermediate host of *Dicranotaenia globosoides* is not an aquatic invertebrate, but some hygrophilous animal.

Choanotaenia crassiscolex occurs both in the species of the genus *Sorex* and in *N. fodiens*. The intermediate hosts of this parasite are various species of snails (*Pulmonata*). The snails infected with the cysticercoids of this tapeworm

were found both in dry and humid biotopes (Table IV). The fact of the general occurrence of the invaded snails in the various biotopes of the BNP explains the possibility of the infection with *Choanotaenia crassiscolex* of mammals which live both in dry and humid biotopes.

On the basis of the Table X it could be supposed that within the genus *Sorex* there is also a specificity towards the species; *Staphylocystis furcata*, *Soricinia tripartita*, *Pseudodiorchis prolifer* and *Hymenolepis scutigera* are recorded in the BNP only in *S. araneus araneus*. At present, however, I am not dealing with this problem, because the latter three species were found for the first time in Białowieża and I studied exclusively the common shrew. May be that they occur also in other representatives of the genus *Sorex*, but they were not hitherto found.

6. Specificity of larvae in intermediate hosts

The intermediate hosts of tapeworms of *Soricidae* (mainly *S. araneus araneus*) hitherto described in the BNP belong to various systematic groups (*Insecta*, *Myriapoda*, *Gastropoda*). However, they have common characteristics: (a) inhabit the same biotopes, (b) have a possibility to contact with the eggs of tapeworms, (c) form common food to the common shrew. Owing to this they are able ecologically to play the role of intermediate hosts of the tapeworms of these mammals.

Limiting myself exclusively to my own material I found that *Choanotaenia crassiscolex* (family *Dilepididae*) developed in snails, and *Staphylocystis furcata*, *Soricinia diaphana*, *Neoskrjabinolepis singularis* and *Pseudodiorchis prolifer* (family *Hymenolepididae*) developed in insects and myriapods. Attention is drawn by the fact that in this case the life cycles of the tapeworms belonging to the same family are specific to the definite systematic groups (types) of intermediate hosts.

Taking into consideration that the larvae of *Staphylocystis furcata* and *Soricinia diaphana* are found in the insect *Geotrupes stercorosus*, the larvae of *Neoskrjabinolepis singularis* in the insect *Catops* sp. and of *Pseudodiorchis prolifer* only in the myriapod *Glomeris connexa* it can be supposed that the specificity of the larvae towards their intermediate hosts can become narrower and can be limited to still smaller systematic units of these animals (genera and even species).

It seems, however, that too few life cycles of tapeworms of insectivorous mammals are known and their systematics (particularly that of the family *Hymenolepididae*), which should reflect the essential phylogenetical relations between the individual species, has too many gaps to analyse accurately this specificity.

On the basis of the present data it can be stated: the common shrews in the BNP are the final hosts of eight tapeworm species producing eggs (the ninth, *Dilepididae* sp., occurs only as the young form). Therefore it can be supposed that the snail, myriapod, or insect, eating the faeces of the common shrew introduce into their alimentary tract the eggs of various species of tapeworms. The fact that only some, specific species reach the body cavity of the given host suggests the presence of a certain specificity of a physiological character.

Hence it can be postulated that the individual tapeworm species adapted itself in the course of the phylogenetic development to some of the several possible, from the ecological point of view, intermediate hosts in which they found suitable conditions for existence. However, the morphological and physiological adaptations of parasites could be found only, according to my opinion, as the result of the establishment of definite alimentary chains which lead to the successive hosts, i. e. in the definite ecological conditions.

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STRESZCZENIE

Celem pracy było: a) zobrazowanie krążenia tasiemców ryjówki aksamitnej (*Sorex araneus* L.) w biocenozie BNP, b) wykazanie zmienności w dynamice tego zjawiska, oraz c) próba wytłumaczenia tej zmienności w oparciu o dane z biologii żywiciela ostatecznego i poznanych dotąd żywicieli pośrednich, na tle czynnika fenologicznego.

W poszukiwaniu naturalnych żywicieli pośrednich tasiemców uwzględniono przedstawicieli trzech grup bezkręgowców: wiję, ślimaki i owady.

Larwy tasiemców znaleziono: u *Geotrupes stercorosus* larwy *Staphylocystis furcata* i *Soricinia diaphana*, u *Pterostichus vulgaris* larwy *Staphylocystis furcata*, a u *Catops* sp. larwy *Neoskrjabinolepis singularis*.

Ponadto u *Geotrupes stercorosus*, *Necrophorus vespilloides* i *Silpha sinuata* znaleziono trzy gatunki cysticerkoidów, jak dotąd niezidentyfikowanych z żadną dorosłą postacią tasiemca.

Łącznie zbadano 2030 osobników *Sorex araneus araneus* L. z czego 1710 (83,9%) zarażonych było tasiemcami.

Prześledzono zmienność ekstensywności zarażenia ryjówki aksamitnej w różnych okresach jej życia oraz w poszczególnych miesiącach roku. Stwierdzono, że u samców intensywność zarażenia jest znacznie wyższa niż u samic.

Prześledzono zmienność składu jakościowego cestodofauny i zagadnienia dominacji poszczególnych gatunków tasiemców i wykazano, że dynamika cestodofauny u ryjówki aksamitnej zależna jest od trybu życia, siedlisk, rodzaju pokarmu i biologii żywicieli pośrednich i ostatecznego, pośrednio zaś od pór roku.

Na podstawie zbadanych dotąd cyklów rozwojowych tasiemców u *Sorex araneus araneus* oraz niektórych innych *Soricidae*, wyróżniono trzy drogi krążenia tych pasożytów: a) przez wiję, b) przez ślimaki, c) przez owady.

Wysunięto przypuszczenie, że specyficzność tasiemców pasożytujących u *Soricidae* w BNP ma charakter ekologiczny, zaś w kształtowaniu się specyficzności postaci larwalnych tych tasiemców do żywicieli pośrednich dominują czynniki fizjologiczne.

